HIGH TEMPERATURE EFFECTS ON FLORAL DEVELOPMENT AND VEGETATIVE GROWTH OF *CHRYSANTHEMUM X MORIFOLIUM* AND THE INVOLVEMENT OF PLANT GROWTH SUBSTANCES

By

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This dissertation is gratefully dedicated

to my parents, Ruby and Roland, and

to my best friend, Bryan.

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HIGH TEMPERATURE EFFECTS ON FLORAL DEVELOPMENT AND VEGETATIVE GROWTH OF CHRYSANTHEMUM X MORIFOLIUM AND THE INVOLVEMENT OF PLANT GROWTH SUBSTANCES

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Pinched plants of Chrysanthemum X morifolium Ramat. 'Orange Bowl' and 'Surf' grown in a chamber maintained at 22° day/18°C night were transferred to 30° day/26° night at the beginning of week 1, 3, 5, or 7 after start of photoinduction period (15-hour nyctoperiod). Plants remained at high temperatures for 2, 4, 6, 8, or 10 weeks and then were returned to the 22°/18° chamber. Exposure to high temperatures during the first 4 weeks of short days caused an increase in number of nodes, leaf area, stem length, and dry weight of leaves and stems. Rate of floret initiation and perianth differentiation decreased when plants of 'Orange Bowl' were exposed to high temperatures during the first 4 weeks of short days. 'Orange Bowl' exposed to high temperatures for 10 weeks from start of short days flowered 12 days later than plants grown at lower temperatures and formed bracteate buds. Flowering of 'Orange Bowl' grown at

22°/18° during the first 4 weeks of short days, then transferred to high temperatures, was not substantially delayed and inflorescences developed normally. Flowering was delayed 3 days when 'Surf' was exposed to high temperatures for 8 weeks from start of short days. Exposure to high temperatures did not cause bracteate bud formation in 'Surf'. With both cultivars, increasing the duration of high-temperature exposure increased time to flowering. Exogenous applications of plant growth substances during floret initiation accentuated or diminished the teratological modifications of supraoptimal temperatures. Cytokinins, gibberellins, and inhibitors of ethylene biosynthesis promoted noninvolucral bract formation on initiated receptacles of 'Orange Bowl' plants. Ethephon (2-chloroethylphosphonic acid) treatments reduced number of noninvolucral bracts. Endogenous zeatin riboside content of induced inflorescences increased with advancing stage of development and increased ambient temperature. Level of 1-aminocyclopropane carboxylic acid (ACC) increased during stage of early floret diffentiation in plants exposed to optimal production temperatures, but supraoptimal temperatures suppressed ACC increase. It appears that gibberellin and/or cytokinin level, activity, or sensitivity may increase in response to supraoptimal temperatures in chrysanthemum causing abnormal inflorescence development, and ethylene appears to be necessary for normal inflorescence development.

CHAPTER I
INTRODUCTION

The chrysanthemum is a herbaceous perennial that has been in cultivation for over 2500 years (30). Today, cultivars of Chrysanthemum X morifolium Ramat. (12) are some of the world's most popular cut flowers and potted ornamental plants. This popularity is due in part to the ability to control year-round commercial availability of the flowers by manipulating daylength and by providing an optimal environment for growth and floral development.

Temperature, irradiance, and photoperiod are the major factors affecting the rate of initiation and differentiation of chrysanthemum inflorescences. Improper photoperiods, low irradiances, and temperatures above or below an optimum can inhibit or delay flowering and may result in abnormal inflorescence formation. It has long been recognized that the effects of temperature on chrysanthemum flowering can be as dramatic as those associated with photoperiod (145). During the winter, irradiance is usually the limiting factor determining rate of floral development; in the summer, high temperature may be limiting and flowering can be delayed. Rate of floral development can be optimized only by proper photoperiod, high irradiances, and controlled temperatures.

In the midwestern and southern United States, high summer temperatures are common, often resulting in delayed flowering and/or poor quality chrysanthemums. This phenomenon is commonly referred to as "heat delay." Although a significant amount of research has been conducted on the influences of temperature on chrysanthemum flowering, detailed information concerning specific developmental stages and the physiological responses affected by

supraoptimal temperatures is not available. The objectives of these studies were to determine the developmental stages most sensitive to high temperatures, to determine the effects of high temperature on vegetative growth, and to investigate the hormonal changes associated with high temperature exposure.

CHAPTER II
REVIEW OF THE LITERATURE

Chrysanthemum X morifolium Ramat. is a member of the family Compositae (Asteraceae), tribe Chrysantheminae (12). The inflorescence is a raceme consisting of a capitulum of marginal ligulate or ray florets (pistillate) and center tubular or disc florets (hermaphrodite) which are initiated centripetally and arranged spirally on the capitulum (110). An involucre of bracts subtends the capitulum which is ebracteate (11). Rate and modifications of capitulum and floret development are affected by environmental conditions and/or chemical treatments (30,41).

Chrysanthemum is a short-day (long-night) plant (6,72) which naturally flowers in the autumn or winter (30,131). Allard (6) and Garner and Allard's (72) discovery that flowering could be manipulated by photoperiod was utilized by Laurie (109) to extend the natural flowering season of the chrysanthemum. Subsequently, Post (138) demonstrated that chrysanthemums could be flowered year-round provided that the daylength was less than the critical photoperiod, the night temperature was controlled, and the cultivars selected carefully.

Cultivars are classified for natural or year-round flowering by response groups which represent the number of weeks of photoinductive short days to attain flower maturation (35). This classification is arbitrary as temperature and irradiance levels affect rate of flower development (16,26). Floral development in chrysanthemum can be divided into three phases: receptacle initiation, floret initiation, and floret development (differentiation). The difference in response

times between cultivars is a function of the rate of floret development, not of receptacle or floret initiation (62).

As a determinate plant, the number of leaves formed prior to the inflorescence is indicative of the rate of inflorescence initiation (38). The onset of flowering (receptacle formation with initiation of involucral bracts [31]) can be observed after three to six consecutive short days depending on cultivar (34,85,142). This response to photoperiod is quantitative (41) since receptacle initiation will eventually occur under noninductive photoperiods (39,40) after the attainment of a critical apical meristem size (36,85). This autonomous induction can be quantified by the initiation of a genetically determined number of leaves (long-day leaf number) characteristic of cultivars (39,45), depending on temperature and irradiance levels (40). Subsequent inflorescence development is quantitative in early-flowering cultivars, summer or garden cultivars (shorter response time) (107,160), but qualitative for late-flowering cultivars, autumn and winter cultivars (longer response time) as anthesis is not attained in these cultivars exposed to noninductive photoperiods (107,142,158).

The critical photoperiod for floret initiation is longer than for floret development (28,70,139), and is dependent on cultivar (response group) (70), irradiance (150), and temperature (28). Generally, the critical photoperiod for floret initiation and development increases with decreasing response times (28,70,178). Increasing the minimum night temperature from 10° to 26.5°C will increase the critical photoperiod for initiation but decrease the critical photoperiod for floret development (28).

Apical inflorescences of chrysanthemums produced under inductive conditions are referred to as "terminal buds"; these inflorescences have fully differentiated florets and are subtended by reproductive lateral shoots (34,137).

Exposure to noninductive photoperiods results in arrested and/or distorted development of the apical inflorescence, a loss of apical dominance, and resumption of vegetative lateral bud growth (30,135,157,158). The resulting arrested and malformed meristems are commonly referred to as "crown buds" (34,135). Crown buds are modifications of terminal buds in which receptacles are initiated, but floret initiation and subsequent floret development are inhibited (34,134,158). Thus, crown buds will form if the photoperiod is extended beyond the critical photoperiod after inflorescence initiation (137,141); on late-flowering cultivars exposed only to long photoperiods; on plants exposed to long photoperiods during which light intensity is limiting (134); or when photoperiods are short enough for receptacle initiation, but too long for floret development (139). If plants are returned to inductive photoperiods, the inflorescences will continue to develop (143,158). Manipulating crown bud formation can be used to improve spray formation (103,140) and to eliminate the need for pinching of cut chrysanthemums (141,142). However, intercalating 10 long days after 11 short days to increase peduncle length on cut chrysanthemums caused bract formation on the receptacles of axillary meristems of 'Hurricane' and 'Statesman', additional disc florets on 'Flame Belair', and secondary inflorescences on 'Pinocchio' (104). Teratological effects have been observed on vernalized plants of 'Indian Summer' exposed for extended periods to noninductive photoperiods, i.e., bracts on the receptacle, secondary inflorescences and petaloid stamens (158).

Temperature can adversely affect chrysanthemum flowering and is of prime importance in commercial scheduling and production of flowers. Temperatures above or below an optimal temperature increase the number of days to flower and, thus, the response to temperature is parabolic (56,98). In the greenhouse, researchers have determined the optimal night temperature to be

approximately 16° for a number of cultivars (27,35,144). Flowering of the cultivar Nob Hill has been shown to occur earlier in plants exposed to 22°/18° (day/night) than in plants at higher or lower temperatures in controlled temperature chambers (19).

The response of chrysanthemum flowering to temperature is cultivar-dependent (26,35,56,144,155,176,181). Cathey (26) categorized chrysanthemum cultivars by flowering response to night temperature. Cultivars were classified as 1) thermonegative--inhibited by high temperatures (maximum 16°), 2) thermozero--unaffected by high or low temperatures (10° to 27°), and 3) thermopositive--sensitive to low temperatures (minimum 16°). In general, late-flowering cultivars are more negatively affected by sub- or supraoptimal temperatures than earlier-flowering cultivars (144).

Discrepancy exists in the literature on the actual inflorescence developmental stages affected by temperature. It has been argued that the response to temperature, similar to photoperiod, is quantitative for floret initiation and qualitative for development (71,144); or the response is quantitative, i.e., sub- or supraoptimal temperatures during induction will delay the rate of initiation and development (56). Post and Lacey (144) hypothesized that high temperatures "counteracted" the short-day photoperiodic influence on flowering in the chrysanthemum cultivars Indianapolis Bronze, Indianapolis Pink, Marie de Petris, and Queen's Lace. They noted that high night temperatures, and to a lesser extent high day temperatures, had a greater effect on rate of inflorescence development than initiation of receptacle and florets (144). Thus, cultivars differed in temperature requirements during inflorescence development, but not during initiation (144). Cathey (27) observed that initiation occurred with exposure to night temperatures of 4° to 27°; however in the thermopositive

cultivar Encore, initiation was accelerated at the higher night temperatures, but continuous high temperatures delayed subsequent inflorescence development. However, Cathey and Borthwick (31) in 1958 suggested that initiation was delayed by increased temperatures. According to these researchers, initiation referred to the time from the start of short days to visible bud, and development was defined as the phase from visible bud to open flower (27,144). These designations are arbitrary and are not indicative of the actual morphological stages. Under continuous lighting, inflorescence initiation in 'Polaris' was delayed at 28° and 10° compared to plants grown at 16° or 22°, and 28° increased the number of leaves formed below the inflorescence (40). However, continuous lighting is inhibitory to floret initiation. Under inductive conditions, Hughes and Cockshull (86) observed that high day temperatures (29.3°) increased the rate of leaf initiation on 'Bright Golden Anne', and receptacle initiation was not delayed. Subsequent inflorescence development was substantially delayed with a decrease in inflorescence dry weight in plants exposed to 29.3° compared to 18.3° day temperature.

In addition to delayed initiation and/or development, high temperatures enhanced vegetative growth (10,19,40,57,86), increased floret number (10,27), induced foliaceous bract formation on the receptacle (144), and arrested inflorescence development precluding anthesis (144). Apparently, the temperature optimum for vegetative growth is higher than the optimum for reproductive development (86). Increased ambient temperatures and irradiances accelerated rate of leaf primordia formation in 'Polaris' (40); and high day and night temperatures increased number of leaves and stem length during long days on eight cultivars (57). 'Escort' chrysanthemums had longer internodes and smaller inflorescence diameters with exposure to increasing temperatures from 15° to 24° during short days (10). Stem length and leaf area of 'Nob Hill' chrysanthemum increased with

increased temperatures (18°/14° to 30°/26°, day/night) in controlled temperature chambers (19). The heat-induced increase in leaf area is apparently the result of a higher percentage of dry matter partitioned to the leaves with a concomitant decrease in partitioned dry matter to the stems (4).

Temperature can have a profound effect on chrysanthemum inflorescence form and color. 'Geisha', a pink-spider type at 14°, developed as a white daisy at 23° (56), and 'Indianapolis Bronze' chrysanthemums grown at 27° night temperatures faded to yellow (136). Increasing temperatures reduced length and width of the ligulate florets of 'Escort' and florets were more tubular (10). Floret number increased with higher temperatures in 'Encore' and 'Escort' (10,27). Moreover, plants produced under high temperatures developed bracts on the receptacle in lieu of florets (144). This modification of a terminal inflorescence is referred to as a bracteate bud, and is distinguished by the presence of noninvolucral bracts on the receptacle; the absence of noninvolucral bracts is a distinguishing characteristic of the tribe Chrysantheminae (158). This characteristic is modified by temperature (144,180) and photoperiod (104,158), and is evidence of interrupted or otherwise perturbed floral development (16).

The relative contribution of day and night temperatures have been debated in the literature. Post and Lacey (144) investigated the effect of high day versus high night temperatures with the following treatments: 16°/16°, 16°/32°, 32°/16°, and 32°/32° day/night, and observed that high night temperature was more detrimental than high day temperatures on flower development, but concluded that both day and night temperatures are important. Cathey (27) also concluded that night temperature had a more profound effect on flowering than day temperature, and thus, averaging of day and night temperatures was not correlated with rate of flower development on 'Encore'. However, the unequal

contribution of night versus day hours was not taken into account in these studies (27); hence, Cockshull et al. (42) proposed that flowering is equally responsive to night and day temperatures. Their work suggests that the mean temperature over a 24-hour period determines rate of flower development (42). Recently, Karlsson and Heins (98) have used response surface analysis to evaluate the relationship between day/night temperatures and photosynthetic photon flux (PPF) on time to flower and plant quality. In their studies on 'Bright Golden Anne', the average temperature hypothesis of Cockshull et al. (42) was not supported; i.e., time to flower for reciprocal combinations of day/night temperatures were dissimilar (98).

High temperatures have been reported to affect flowering in many genera. Total leaf number increased in seedlings of Nicotiana tabacum L. 'Coker 319' when exposed to increasing temperatures (18°/14° to 30°/26°, day/night) with a concomitant delay in flower initiation (170). The photoperiodic response is profoundly altered in common cocklebur (Xanthium strumarium L.) by night temperature, as temperatures of 38° suppressed floral initiation under inductive photoperiods (78). High night temperatures (21°) inhibited bud differentiation in Gardenia veitchii Hort. compared to low temperatures (13° to 16°) (101). High temperature (28°/23°, day/night) exposure during flower development reduced the number of petals, stamens, carpels and locules in tomato (Lycopersicon esculentum Mill.) compared to low (18°/15°) or intermediate (23°/18°) temperature treatments (156). Pretransplant high temperature treatments (25°, 30°, or 35° for 10 to 20 days) inhibited bolting, i.e. inflorescence stalk elongation, and promoted vegetative growth in spring-harvested celery, Apium graveolens L. 'Florida 683', grown under inductive conditions of low temperatures (147).

In chrysanthemum, responses to environmental cues have been shown to be mediated by endogenous plant growth substances. Tompsett and Schwabe (173) suggested that flowering responses to environmental cues are regulated by absolute concentrations and interactions of endogenous plant growth substances. However, variations in levels of endogenous plant growth substances hypothesized to be the promoters or inhibitors of flowering may rather be the consequences of floral induction.

Bioassays have indicated that 'Shasta' chrysanthemums contain more growth promoting substances (auxins) when grown under long days, and contain higher growth inhibitor levels during short days (79). Tompsett and Schwabe (173) observed that inflorescences of 'Sunbeam' chrysanthemums subjected to long photoperiods contained higher auxin and abscisic acid levels and lower auxin oxidase levels than plants subjected to photoinductive short photoperiods. Gibberellin level increased with exposure to short days (173). Exogenous applications of IAA (indol-3yl-acetic acid) or NAA (1-napthaleneacetic acid) during the first 4 weeks of photoinduction delayed flowering while GA_3 (gibberellic acid) applications promoted flowering in chrysanthemum cultivars Yellow Spider, Yellow Giant Indianapolis, and White Bonnie Jean (165). Daily IAA sprays during short days inhibited flower bud initiation, as indicated by a 2-fold increase in leaf number, and inhibited subsequent flower bud development in 'Iceberg' (114). However, the response to applied auxin is rate-dependent as low or high concentrations may promote or inhibit flower induction, respectively (37,111). Induced inflorescences of 'Indian Summer' can be inhibited in their development by exposing them to long days, low irradiance levels, or by application of auxin paste (158). Sensitivity to auxin applications decreased with advanced stages of floret development in 'Hurricane' and 'Indian Summer' (75,158) with ovule

formation being the latest stage affected (158). Thus, high endogenous auxin levels may be responsible for inhibition of floret development of chrysanthemums exposed to noninductive photoperiods (158).

Exogenous applications of IAA have also been shown to inhibit flower induction and development in other plant species (76). Auxin activity in common cocklebur was higher when plants were exposed to noninductive photoperiods and activity declined with the appearance of floral primordia (47). IAA applied to the plumules of pigweed (Chenopodium rubrum L.) before or during photoinduction inhibited DNA synthesis and meristematic activity (161). The axillary meristems were affected the most, since apical dominance was promoted, and consequently floral differentiation was inhibited.

In whole root extracts of chrysanthemum 'Polaris', zeatin- and zeatin riboside-like compounds are the major endogenous cytokinins (100) and were detectable throughout the flowering process (83). There is no conclusive evidence, via agar-diffusive studies, that cytokinins are synthesized or produced in chrysanthemum shoot tissue (124). The principal site of cytokinin synthesis is considered to be the root tip (15). There is a close correlation between developmental processes in the shoot tip and the quantities of cytokinins translocated from the roots (15,53). For example, during flower initiation and development in Perilla frutescens (L.) Britt., a short-day plant, acropetal translocation and activity of cytokinins in xylem sap increased to 5 times that of noninduced plants (15). The synthetic cytokinin, 6-benzylamino-9-(tetrahydropyran-2-yl)-9H-purine (PBA), applied to chrysanthemum 'Bright Golden Anne' inflorescences prior to floret initiation increased diameter and fresh weight of the inflorescence with efficacy decreasing with advanced development (93). Carnation (Dianthus caryophyllus L. 'White Sim') flowers treated with PBA

developed a greater number of petals and secondary growth centers which resulted in "bullhead" flowers (93). There was not an increase in chrysanthemum 'Bright Golden Anne' floret number as a result of PBA applications (93). Inflorescence dry weight and floret number increased with BA (6-benzyladenine) treatments to inflorescences of Leucospermum sp. R. Br. 'Red Sunset' applied during induction (129). Jeffcoat (93) hypothesized that PBA may be enhancing transport of assimilates to the inflorescence or affecting the water balance in the inflorescence. Indeed, cytokinins may be responsible for changes in the import ability of strong sinks such as inflorescences. Assimilate accumulation in the shoot apices axes increased and inflorescence development was promoted in response to short-day photoinduction, removal of youngest leaves, or PBA (N-benzyl-α-[tetrahydro-2H-pyran-2yl]-adenine) treatments in Bougainvillea sp. Comm. ex Juss. 'San Diego Red' plants (175). Apparently the youngest leaves were competing sinks for assimilates, and cytokinin applications to the shoot apices or short days increased sink strength prior to morphological changes (175). Thus, short days may affect assimilate translocation by affecting cytokinin synthesis and/or distribution (175,177).

Cytokinins may be inhibitory to flowering. Davey and van Staden (54) observed a decrease in cytokinin activity of white lupin root exudate, Lupinus albus L., with the onset of flower development and activity continued to decline during flower maturation. In tomato, zeatin and zeatin riboside activity decreased in the root exudate as flower development occurred (53). A dramatic decrease in the level of cytokinins was observed in buds of common cocklebur in response to short-day treatment (177), which lead to the hypothesis that the reduction was requisite to subsequent flowering (82). During early flower development in Cosmos sulphureus Cav., cytokinin activity in the flower buds was lower than at

flower opening (152). A decrease in cytokinin activity in reproductive meristems or undetectable levels may suggest that cytokinins are being rapidly metabolized. However, kinetin applications to plumules of pigweed exposed to photoinductive short days promoted apical meristematic activity stimulating vegetative leaf growth and suppressing flower differentiation which indicated that the promotion of leaf growth by kinetin applications correlatively inhibited flower bud development (163).

There is no simple correlation between flowering and endogenous gibberellins (133). GA_3 applications promoted flower bud initiation in the qualitative short-day plant Impatiens balsamina L. under noninductive photoperiods, and repeat applications stimulated subsequent development (128). However, GA_3 applied to apical buds of the long-day plant Fuchsia X hybrida Hort. ex Vilm. 'Lord Byron' inhibited flower initiation (151). Gibberellic acid suppressed flower initiation in the short-day plant Fragaria sp. L. 'Talisman' maintained under short days, and plants resembled plants produced under long days (171). In bougainvilla, a short-day plant, gibberellic acid inhibited inflorescence development similar to effects of noninductive photoperiods, low light level, and high night temperatures (148). Flower development was delayed in plants of Euphorbia pulcherrima Willd. (poinsettia) by spray applications of gibberellic acid under inductive short days (77). Moreover, there may be inhibitory and promotive effects of applied GA's within a species; GA_3 applications to Pharbitis sp. L. is promotive prior to photoinduction, but inhibitive after photoinduction (133). These differences may be attributable to tissue specificity and changes in sensitivity to endogenous phytohormones.

In chrysanthemum, the effect of exogenously applied or endogenous gibberellins on flowering may involve the distribution of assimilate (121). Jeffcoat

and Cockshull (94) found that activity of gibberellin-like substances in 'Bright Golden Anne' directly correlated with the relative growth rates of the inflorescence. When inflorescences were at their maximum relative growth rate (time of highest sink demand), the amount of gibberellin-like substances, as determined by bioassays, were at maximum levels (94). Gibberellin levels declined with the decline of the inflorescence's relative growth rate, concomitant with decline in sink strength. Cathey and Stuart (32,168) showed that gibberellins did not affect receptacle or floret initiation in short-day treated chrysanthemums as leaf number prior to inflorescence initiation was unaffected. Applications during differentiation and later development reduced time to anthesis in 'Shasta' and 'Indianapolis Yellow' chrysanthemums (32,168), and rate of flower bud development in chrysanthemums grown under inductive photoperiods with initiated florets was promoted by applications of gibberellins (32,121-123,125,168). Weekly exogenous applications of gibberellins alone or in combination with BA promoted inflorescence development in 'Pink Champagne' chrysanthemums grown under noninductive photoperiods (132). GA and BA effects were synergistic, however, anthesis was not attained for any treatments, and IAA was inhibitory (132). Thus, gibberellins are viewed as required promoters of inflorescence development in chrysanthemums (121).

The growth retardants chlorphonium chloride, daminozide and piproctanyl bromide delayed inflorescence development but not inflorescence initiation in chrysanthemum 'Bright Golden Anne' grown under inductive photoperiods (121). Ancymidol has been demonstrated to inhibit flower development in a dose-response manner in 'Nob Hill' plants maintained in controlled environments (19). The effect of growth retardants on reducing gibberellin levels may be a reduction in translocation of assimilate to the rapidly developing inflorescence, thus delaying

development (121). This delay can be reversed by gibberellin applications which attract assimilates to the inflorescence, and thus accelerate development (121,123,125).

This apparent role for gibberellins in flower development has also been demonstrated in rose and carnation. In 'White Sim' carnations, cytokinins (166) and gibberellins (95) diverted assimilates to the application site, and hence promoted flower development (81). Removal of the carnation flower resulted in altered assimilate transport towards the roots. However, applications of GA_3 or IAA to the decapitated stem, redirected the assimilates upward (95). GA_3 applied to receptacles of developing 'Baccara' rose (Rosa sp. L.) flowers increased flower size, dry weight, and pigmentation (190) probably by augmenting sink strength (190,193). Endogenous gibberellin levels were lower in leaves of abortive shoots than flowering shoots (191), and low light and temperature conditions promoting bud atrophy decreased endogenous gibberellin level (193). Gibberellin applications to developing rose flowers reduced, and ethephon applications increased flower bud atrophy (192). Cytokinin (BA or PBA) treatments decreased endogenous gibberellin activity and resulted in increased incidence of bud atrophy; however, GA_3 applications counteracted the cytokinin effects (194).

Differential reponses to exogenous abscisic acid (ABA) on flowering have been reported (67). Endogenous ABA levels were higher in chrysanthemum '#3 Indianapolis White' exposed to short days compared to long days (164). Tompsett and Schwabe (173) postulated that this increased level of ABA may inhibit the growth of other plant parts during inflorescence development. Daily applications of ABA did not affect flowering, stem length, or number of nodes on chrysanthemum 'Fred Shoesmith' (29). However, applications of ABA to induced pigweed plants were inhibitory to floral differentiation (162).

Ethylene or ethylene-releasing compounds promoted flower induction in pineapple (Ananas sativa L. [48] and Ananas comosus L. Merr. [37]), various ornamental bromeliads (Aechmea fasciata [Lindl.] Bak., Neoreglia sp. L. B. Sm., and Vriesea splendens [Brongn.] 'Lemaire') (33), and Belgian endive (Cichorium intybus L. 'Foliosus') (58); induced flowering in the qualitiative short-day plant Plumbago indica L. 'Angkor' grown under noninductive photoperiods (130); and enhanced flower initiation in young apple (Malus sylvestris Mill. 'Delicious') trees (182). Aechmea victoriana L. B. Sm. plants were induced into flower by ethylene or ACC (1-aminocyclopropane-1-carboxylic acid) treatments, but plants must be at a stage of "flower maturity" which coincides with an increase in the tissue's capacity to convert ACC into ethylene (55). Moreover, flower induction in the bromeliad Guzmania lingulata (L.) Mez. 'Minor' is positively correlated with endogenous ethylene production (59). Flower induction was retarded in Bromeliaceae by the ethylene biosynthesis inhibitor, AVG, L-2-amino-4-(2-amino-ethoxy)-trans-3-butenoic acid hydrochloride (aminoethoxyvinylglycine) (120). MVG, L-2-amino-4-methoxy-trans-3-butenoic acid, and AVG delayed flower development in Nemesia strumosa Benth. (116). In the long-day plant, Spinacia oleracea L., leaf and whole-plant ethylene production rates were significantly increased by photoinductive treatments compared to noninductive daylengths (50). ACC was more concentrated in leaves from noninduced plants, indicating that induced plants had a greater capacity for ACC conversion (50).

However, in many plants, ethylene inhibits flower formation (189). Treating peach trees, Prunus persica (L.) Batsch. 'Redglobe', with ethylene-generating compounds, ethephon and CGA-15281 (Ciba-Geigy, Ltd.), in the late summer or fall delayed flowering the following spring (49). Ethylene applications to cotyledons of the short-day plant Pharbitis nil L. 'Violet' during the inductive

dark period were effective in inhibiting floral induction (169). Ethephon treatments to burley tobacco (Nicotiana tabacum L.) while in seed beds suppressed premature flower induction and resulted in higher yields (99). Under inductive short days, foliar applied auxins inhibited flower initiation and development in common cocklebur (21); while application of triiodobenozoic acid (TIBA) or 2,4-dichloranisole (DCA) under non-inductive long days induced flower bud initiation (20). Ethylene inhibits floral induction in common cocklebur (2), thus the effect of IAA on flowering in cocklebur is probably via its effect on ethylene production.

Inflorescence initiation and development in chrysanthemum '#3 Indianapolis White' exposed to short days is inhibited by continuous ambient applications of 1 to 4 ppm ethylene, and intermittant applications resulted in crown bud formation (172). Plants subjected to ethylene under long or short photoperiods had thickened stems, shortened internodes, epinastic leaves, and a loss of apical dominance (172). Ethylene-treated plants which failed to flower under short days had higher levels of inhibitors (auxin) as determined by bioassays (172). Low concentrations of ambient ethylene (1 ppm) appeared to inhibit chrysanthemum inflorescence development more than initiation (146). Ethephon sprays during short days inhibited inflorescence development and lowered ABA levels compared to untreated plants ('#3 Indianapolis White') exposed to short or long days (164). Plants of 'Polaris' treated with 100 or 1000 ppm ethephon at start of short days were delayed in flower initiation and more leaves were formed below the inflorescence; and ethephon treatments during long days inhibited inflorescence initiation to a greater extent than in untreated plants (43). Rate of leaf initiation and leaf number were increased by ethephon applications; moreover, apical dominance was modified as leafy axillary shoot development was

promoted (43). The number of leaves formed on plants treated with ethephon in long or short days were similar, indicating that the effect was probably independent of long-day inhibition of initiation (43). The practical application of this ethylene effect is use of ethephon to inhibit premature and irregular budding on garden-type cultivars which bud readily in long days (44).

Ethylene production in vegetative tissues is significantly affected by exogenously applied plant growth substances (1). It has long been recognized that auxin promotes ethylene production (197). Tissues treated with IAA contained 100 times ACC and ethylene production was stimulated 500 times compared to untreated mungbean (Vigna radiata [L.] R. Wilcz.) hypocotyls (187). In subapical hypocotyl segments from 3-day old etiolated mungbean seedlings, IAA treatment increased ACC synthase activity, and BA further enhanced IAA-induced activity (184). Auxin induces ethylene biosynthesis in mungbean hypocotyls by inducing ACC synthase and the induction is time- (187) and concentration-dependent in pea (Pisum sativum L. 'Alaska') seedlings (97) and in mungbean hypocotyls (153). The conversion of SAM (s-adenosylmethionine) to ACC is the rate-limiting reaction in ethylene synthesis (183). IAA apparently stimulates de novo synthesis of ACC synthase since IAA-induced ethylene production is suppressed by inhibitors of RNA and protein synthesis and there is a considerable lag period prior to IAA-stimulated ethylene production (1,3,23,153,185). Furthermore, AVG, which inhibits ACC synthase (5,18), eliminated ACC accumulation and auxin-induced ethylene production (187). Ethylene treatment inhibited the incorporation of ^{3}H-thymidine into DNA in pea roots and apices and is thus a possible mechanism by which ethylene inhibits cell division (7). The inhibitory action of auxin on cell division in primary meristematic tissues may be attributed to auxin-induced ethylene production (7).

Kinetin applications are synergistic to auxin-induced ethylene production (24,69). Application of cytokinin (BA or kinetin) was synergistic to IAA-induced ethylene production in 2- to 5-day old 'Alaska' pea, radish (Raphanus sativus L. 'Early Scarlet Globe'), bean (Phaseolus vulgaris L. 'Tendergreen Improved'), cucumber (Cucumis sativus L. 'Boston Pickling'), and maize (Zea mays L. 'Golden Bantum') seedlings (69). Gibberellin applications did not affect ethylene production (69). In mungbean hypocotyl segments, cytokinin (BA or kinetin) applications increased ethylene production with and without IAA (89,105). Kinetin may be affecting ethylene production by regulating the free endogenous IAA level via suppression of auxin conjugation in urd (Phaseolus mungo L.) hypocotyl segments (108), as a higher level of free IAA is correlated with higher endogenous ethylene production (97,108). However, tracer experiments indicated that the increase in free endogenous IAA as a result of cytokinin treatments was insufficient to account totally for the observed increase in ethylene production (89). It has been proposed that cytokinins may affect ethylene production directly, similar to IAA regulation (183).

There is evidence of mutually antagonistic effects involving ethylene and other plant growth substances. In lateral buds released from apical dominance, and in roots and shoots of seedlings of 'Alaska' pea, cell division was suppressed at a stage prior to prophase as a consequence of exposure to ethylene; this inhibition of mitosis was partially reversed by BA applications (7). Coleus (Coleus blumei Benth.) roots treated with ethephon had decreased cytokinin activity levels in the root exudate and root growth was inhibited (13). BA treatment of cut carnation delays senescence by affecting ethylene synthesis and action (46). Researchers have demonstrated antagonistic responses by gibberellin and ethylene applications in 'Alaska' pea seedlings (69) and lettuce (Lactuca sativa L.)

hypocotyl elongation, invertase activity in sugar beet (Beta vulgaris L.) tissue, and α-amylase activity in barley (Hordeum vulgare L.) endosperm (159). Daminozide treatments to 'Ingrid Marie' apple shoot tips decreased shoot growth and increased rate of ethylene production (96). ABA inhibited methionine to ethylene conversion in 3-day old 'Alaska' pea seedlings (74) and in etiolated mungbean hypocotyls (105). Furthermore, ABA suppressed IAA-induced ACC synthase activity and inhibited ethylene production in etiolated mungbean hypocotyls (184). Therefore, it is probable that auxin, BA and ABA influence ethylene production by regulating endogenous ACC synthase activity (184).

In response to environmental stimuli, plant growth substances may regulate ontogenetic development both spatially and temporally via assimilate transport and distribution (174,179). Sachs and Hackett (148,149) have proposed that growth substances may control floral initiation and development by regulating the partitioning of assimilates. Thus, plant growth substances may be acting indirectly upon flowering by influencing assimilate partitioning by affecting relative sink strengths, hence, competition between critical meristematic regions (apical versus subapical) or within the apex rather than directly as morphogenetic or gene modulators (149). The control may be at the level of regulation of activities in the sink tissue or at the translocation mechanism (127). Recent evidence suggests that plant growth substances may directly control phloem loading of sucrose (52). But, Bodson and Bernier (17) have debated that changes in carbohydrate status are requisite for flower initiation but are not the sole controlling factors in flower initiation.

There is ample evidence that the effect of temperature on flowering may involve photosynthate production, translocation, and/or accumulation. High bud temperatures (21° to 30°) in 'White Sim' carnations increased accumulation of

^{14}C-labelled assimilates in the flower at the expense of the stem, and localized cooling of the bud (10° to 0°) decreased the translocation of assimilates into the flower (80). Rate of shoot apex enlargement was decreased and rates of leaf formation and growth increased in 'Potentate' tomato seedlings maintained at constant temperatures of 25° compared to constant 15° (87). The delay in apex enlargement and the increase in leaf number prior to flowering in response to elevated temperatures was hypothesized to be a function of competition for available assimilate, i.e. the sink strength of the leaf primordia being greater than that of the apex when exposed to higher temperatures (87). Removal of the first two expanding leaves of tomato seedlings exposed to the high temperature (25° constant) treatment resulted in a rapid expansion of the shoot apex and earlier flower initiation (88). However, defoliation of low temperature (15° constant) treated plants caused a slight increase in apex size but had no effect on rate of flowering (88). On the basis of these studies, Hussey (88) concluded that the first two leaves competed strongly with the shoot apex for assimilates when exposed to supraoptimal temperatures. Assimilate partitioning in the tomato cultivars Roma VF and Saladette, high temperature sensitive and tolerant, respectively, was reduced in response to exposure to heat stress conditions, (38°/25°, day/night, for 48 hours) compared to plants exposed to control (26°/15°) temperatures since carbon export from source leaves (61) and acropetal movement and import of assimilates into young floral buds were reduced (60). Tomato flower set is most sensitive to high temperatures 3 to 4 days after flower initiation which apparently involves the sink demand of the inflorescence (60). Moreover, high temperatures (35° to 40°) were shown to decrease carbon fixation to a greater extent in the heat-sensitive cultivar Roma VF compared to heat-tolerant 'Saladette' (14).

Plant growth substances may regulate the responses to heat stress (92). The primary response to heat stress may be an alteration in membrane integrity causing phytohormone imbalances (92). However, it is not known whether differences in hormonal activity represent the cause or an effect of heat tolerance. The studies of high temperatures and cytokinin response constitute the vast majority of evidence (119). Cytokinins synthesized in the roots have been suggested to be "protective substances" in heat-stressed plants due to their antioxidant activity and involvement with protein synthesis (112). Roots of wheat (Triticum aestivum L. 'Svenno Varvete') died at temperatures of 35°-36°; however, pretreatment with ethanol or kinetin protected the wheat roots against supraoptimal temperature injury (167). In leaves of intact plants of the Christmas begonia (Begonia X cheimantha Everett 'Prinsesse Astrid') cytokinin activity was higher at 18° than at 21° or 24°, as determined by bioassay, with a concomitant decrease in adventitious bud formation at the higher temperatures (195). Using bioassays, Cole (Ph.D dissertation cited by McDaniel [119]) observed inhibition of cytokinin synthesis or translocation as a result of high root temperatures; and the temperature tolerant 'Wando' pea maintained higher cytokinin activities in response to high temperature exposure (40° for 9 days) than temperature sensitive 'Alaska'. Cytokinin, gibberellin, and ABA activity as determined by bioassays were determined in stem xylem exudate from 'Inra 200' maize exposed to root temperatures of 18°, 23°, 28° or 33° (9). Highest rate of cytokinin and gibberellin export from the roots occurred at 28° and both decreased sharply with increased temperature (33°) exposure (9). Greatest rate of ABA export from the roots occurred at 13°-18° with decreases at higher or lower temperatures (9). A heat treatment (47.5° for 2 minutes) to roots of 'Fronica' maize seedlings also reduced endogenous cytokinin levels 6-fold as determined by a zeatin riboside-Ab

radioimmunoassay; and BA treatments to the corn seedlings reversed heat stress inhibition of photosynthesis, chlorophyll accumulation, and chloroplast development (25). Xylem (root) exudate from topped 'Great Northern' bean plants exposed to 46° or 47.5° for 2 minutes increased 4-fold in ABA content and decreased 6-fold in cytokinin activity concomitant with changes in membrane permeability and ion uptake (92). Sublethal high temperature treatments (46°-49° for 2 minutes) to roots and shoots of wild tobacco (Nicotiana rustica L.) increased ABA levels and initially decreased cytokinin levels in leaf exudate similar to effects of water stress (90). Pretreatment of tobacco seedlings with ABA or kinetin enhanced recovery from heat shock (91), i.e., the effects of the high temperature treatment: onset of senescence, inhibition of protein synthesis or promotion of proteolysis, were reversed by kinetin applications (90). Levels of free ABA in shoots of 'Venus' tomato seedlings exposed to low (15°/10° or 10°/5°, day/night) or high (35°/25° or 45°/35°) temperatures were increased compared to levels in seedlings exposed to optimal temperatures of 25°/15° (51). No differences in leaf water potentials were observed between the temperature treatments (51). Hence, the increase in ABA levels in response to temperature stress may be involved in enhancing plant temperature tolerance by modifying tissue water balance (51). Auxin-like substance and auxin "oxidase" activities were higher at 28° than 20° in chrysanthemum 'Sunbeam' exposed to short days (173). However, auxin and gibberellin activities were reduced by exposure to high (38°) temperatures for 5 hours in tomato floral buds compared to control temperatures (24°-28°/17°-22°, day/night) (106).

The optimum temperature for ethylene production in plant tissues is approximately 30° (186). Ethylene production is inhibited at temperatures above 35° in many fruits, and this inhibition is probably responsible for the problems

associated with fruit ripening at elevated temperatures (22). Ethylene production, as determined by gas chromatography, was inhibited above 20° and 30° for tomato and common apple (Malus domestica Borkh), respectively (118). Abnormal ripening of avocado (Persea americana Mill. 'Hass') fruit at temperatures above 30° was the result of a significant reduction in ethylene production due to increasing temperatures (64). Avocado fruit maintained at 35° or 40° did not produce appreciable quantities of ethylene and at 40° a climateric was not observed (64). Increasing incubating temperatures from 25° to 35° increased ethylene production twofold, but temperatures above 37.5° significantly reduced basal and wound (stress-induced) ethylene production in leaf discs from 'Masterpiece' dwarf bean, with complete inhibition at 45° and above (68).

The reaction rate of the conversion of ACC to ethylene was retarded by temperatures above 29° in 'Golden Delicious' apple fruit tissue slices (8). Yu et al. (186) demonstrated that high temperatures (35°) primarily affected the conversion of ACC to ethylene in 'Golden Delicious' apple plugs and auxin-treated mungbean hypocotyls, and that synthesis of ACC was less sensitive to high temperature inactivation. However, Horiuchi and Imaseki (84) observed that ACC synthase activity induced by IAA was more sensitive to high temperatures (40° and above) than the conversion of ACC to ethylene in etiolated subapical hypocotyl sections of mungbean. In addition, percent inhibition of ethylene biosynthesis by rhizobitoxine, L-2-amino-4-(2-aminoethoxy)-trans-3-butenoic acid, in common apple plugs increased with increasing temperatures (118).

Inhibition of ethylene biosynthesis by high temperatures may be caused by pertubations in cellular membranes, i.e. alterations in conformation of membrane-bound enzymes and/or membrane integrity. Stable, intact functional membranes are requisite for ethylene biosynthesis (8,113). In subapical stem sections of

etiolated 'Alaska' pea seedlings, wound ethylene production increased from 24° to 36°, with a dramatic decrease at temperatures above 36°, indicative of a requisite of membrane integrity for ethylene production (154). Membrane involvement is also suggested from discontinuous Arrhenius plots of temperatures versus ethylene production (118). Field (68) proposed that a loss in the integrity of the ethylene production system was the result of temperatures above 37.5° as an increase in electrolyte leakage correlated well with reductions in ethylene production. Field (68) concluded that high temperatures altered membrane integrity and thus adversely affected the activity of the membrane-bound enzymes of ethylene synthesis. Furthermore, environmental effects on membrane function may also involve de novo synthesis of ACC synthase (117).

CHAPTER III
HIGH TEMPERATURE EFFECTS ON FLORAL DEVELOPMENT AND VEGETATIVE GROWTH OF CHRYSANTHEMUM X MORIFOLIUM

Introduction

High temperatures during production can delay flowering and induce abnormal inflorescence development in chrysanthemums (144). This phenomenon is commonly referred to as "heat delay" and has been shown to be induced by temperatures in the range of 27° to 32°C (27,31,40,144). The severity of heat delay depends to a large extent on the tolerance or sensitivity of various chrysanthemum cultivars to high temperatures.

Discrepancy exists in the literature on the effects of high temperatures on chrysanthemum growth and floral development. Based on dates of visible bud and flowering, Post and Lacey (144) reported that high temperatures did not affect "bud initiation" (time from start of short days to visible bud), but delayed "bud development" (time from visible bud to flower). Moreover, they observed bract formation and a "large number" of developed florets on the capitulum in response to high temperatures. Cathey (27) found that high temperatures enhanced "bud initiation" but delayed "bud development." However, Cathey and Borthwick (31) later reported that floral initiation was slightly delayed by increased temperatures. Cockshull (40) has observed an increase in leaf production and a delay in capitulum initiation in response to high temperatures; however, these studies were conducted under continuous lighting which precluded floret initiation. The objectives of the present study were to determine the most sensitive stage(s) of floral development, to determine the effects of high

temperature on vegetative growth, and to investigate the effect of high-temperature duration by comparing a sensitive to a tolerant cultivar.

Materials and Methods

Rooted chrysanthemum cuttings of 'Orange Bowl' (10-week-photoperiodic response, high temperature sensitive) and 'Surf' (9-week-photoperiodic response, high temperature tolerant) were planted in a soilless growth medium (Metro Mix 300, W.R. Grace Co., Cambridge, MA) in 225-ml styrofoam cups. Plants were placed in a chamber (8.9 m^2) in the Southeastern Plant Environment Laboratory (phytotron) at North Carolina State University, Raleigh, NC, at a plant density of 86.5 plants m^{-2}. Cool-white fluorescent and incandescent lamps provided a photosynthetic photon flux (PPF) of approximately 640-650 μmol s^{-1} m^{-2} for 9 hr per day. Plants were exposed to a 3-hour night interruption (2300-0200 hr) of 11-12 μmol s^{-1} m^{-2} from incandescent filament lamps (63). Two weeks after planting, short-day photoinductive periods were initiated by providing a 15-hr nyctoperiod from 1700 to 0800 HR. Ambient temperatures of 22±0.25°C day and 18±0.25° night were maintained in one chamber, which served as the low temperature or control chamber, and another chamber maintained at 30±0.25° day and 26±0.25° night was used for the high temperature treatments. Temperatures were monitored with a type T (copper-constantan) thermocouple in a shielded aspirated housing (63). Temperatures selected for this study were based upon a previous study conducted in the phytotron which involved exposing plants of both cultivars at the start of short days to day/night temperatures of 18°/14°, 22°/18°, 26°/22° and 30°/26° until stage of flower maturation (unpublished data).

Plants were irrigated daily with 300 ml per plant of a modified Hoagland's solution (7.6 mM nitrogen) and 300 ml deionized water (63). Plants were pinched one week after planting and pruned to one lateral shoot when shoots were 3 cm

in length. Leaves below the pinch were pruned to four per plant for 'Orange Bowl' and five per plant for 'Surf'. Plants were randomly divided into 15 subgroups (treatments) for 'Orange Bowl' and 11 treatments for 'Surf'. Treatments consisted of exposing plants to high temperatures at the start of short days (week 1) or 2 (week 3), 4 (week 5), or 6 weeks (week 7) after the start of short days for 2, 4, 6, 8, or 10 weeks (Table 3-1). Cultivars were in separate experiments which were incomplete factorials in a randomized complete block design with three replicates over time (three plantings 1 week apart) using six plants per replicate/treatment/cultivar.

Leaf area, stem length, and leaf, stem and inflorescence dry weights of the lateral shoot were recorded each week for two plants per treatment/replicate. Number of short days to flower color (showing-color) and to when the outer rows of florets were perpendicular to the pedicel (open-flower) were recorded. Inflorescences were evaluated for abnormal development, floret color, and number of florets at open flower.

At 3, 7, 11, 15, 19, 23, and 27 days after the start of short days, six meristems from plants exposed to either low or high temperatures from the start of short days were fixed in formalin-glacial acetic acid-95% ethanol (FAA) and observed with a dissecting light microscope. Meristem diameter, appearance of involucral bract primordia, number of rows of initiated florets, and number of rows of florets with differentiated perianth were recorded. For electron microscopy, selected meristems were dehydrated in a graded alcohol series, critical point dried, coated with Au/Pd in a Technics Hummer V sputter coater, and viewed with a Hitachi S-450 scanning electron microscope.

Table 3-1. Duration and timing of high temperature treatments that were used on 'Orange Bowl' and 'Surf' chrysanthemums.

	Number of short days after start of short days					
Treatment[z]	1	14	28	42	56	70
1-2	xxxxxxxxxxx[y]					
1-4	xxxxxxxxxxxxxxxxxxxx					
1-6	xxxxxxxxxxxxxxxxxxxxxxxxxxxx					
1-8	xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx					
1-10[x]	xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx					
3-2		xxxxxxxxxx				
3-4		xxxxxxxxxxxxxxxxxxx				
3-6		xxxxxxxxxxxxxxxxxxxxxxxxxxxx				
3-8[x]		xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx				
5-2			xxxxxxxxxx			
5-4			xxxxxxxxxxxxxxxxxx			
5-6[x]			xxxxxxxxxxxxxxxxxxxxxxxxxxxxxx			
7-2				xxxxxxxxxx		
7-4[x]				xxxxxxxxxxxxxxxxxx		

[z]First number refers to week at which high-temperature treatments were initiated and the second number refers to length in weeks of high temperature exposure.
[y]Duration in high temperature chamber.
[x]'Orange Bowl' only as 'Surf' is classified as a 9-week response cultivar and 'Orange Bowl' is classified as a 10-week response cultivar.

An additional study was conducted simultaneously at the Ornamental Horticulture Department Greenhouses of the University of Florida, Gainesville, FL. Cultivars and treatments were identical to the experiment previously described. As the results obtained from this study were similar to those of the phytotron, only the phytotron results will be reported.

Results and Discussion

Effect of High Temperature on Vegetative Growth

High temperature treatments initiated at the start of short days or at week 3 (treatments 1-2, 1-4, 1-6, 1-8, 1-10, 3-2, 3-4, 3-6, and 3-8) increased leaf and stem dry weights in 'Orange Bowl' compared to the control (Table 3-2). High temperature treatments initiated at week 5 or 7 (treatments 5-2, 5-4, 5-6, 7-2, and 7-4) did not substantially increase lateral shoot dry weights compared to the control. At open flower, stem and leaf dry weights accounted for 51% and 74% of the total lateral shoot dry weight for 'Orange Bowl' plants exposed to low and high temperatures for the entire short day period (control and treatment 1-10), respectively.

Stem and leaf dry weights of 'Surf' plants were greater when exposed to high temperatures at the start of short days (treatments 1-2, 1-4, 1-6, and 1-8) compared to plants exposed to high temperatures after week 3 or remaining at low temperature until open flower (Table 3-3). Stem and leaf dry weights of 'Surf' plants exposed to low or high temperatures (control or treatment 1-8) accounted for 46% and 62% of total lateral shoot dry weight, respectively. The increase in shoot dry weight in both cultivars was attributable to an increase in leaf and stem growth as temperature treatments had little effect on final inflorescence dry weight (Tables 3-2 and 3-3).

Table 3-2. Effect of high- (30°/26°C) and low- (22°/18°) temperature treatments during short days on leaf, stem, and inflorescence final dry weights of the lateral shoot for 'Orange Bowl' chrysanthemums.

	Orange Bowl			
Treatment	Leaf dry weight (g)	Stem dry weight (g)	Inflorescence dry weight (g)	Total dry weight (g)
1-2[z]	1.17	1.05	1.60	3.81
1-4	1.74	1.51	1.38	4.63
1-6	1.89	1.61	1.26	4.76
1-8	1.58	1.49	1.13	4.20
1-10	1.57	1.46	1.19	4.22
3-2	1.16	0.97	1.07	3.19
3-4	1.29	1.07	1.12	3.47
3-6	1.16	1.06	1.20	3.43
3-8	1.14	1.11	1.16	3.41
5-2	0.88	0.75	1.30	2.93
5-4	0.93	0.73	1.07	2.73
5-6	0.92	0.75	1.21	2.88
7-2	0.82	0.69	1.48	3.00
7-4	0.81	0.59	1.39	2.79
Control	0.76	0.66	1.37	2.78
Waller-Duncan at 5% level	0.37	0.25	0.47	0.54

[z]First number refers to week at beginning of which high-temperature treatments were initiated and second number refers to length in weeks of high-temperature exposure.

Table 3-3. Effect of high- (30°/26°C) and low- (22°/18°) temperature treatments during short days on leaf, stem, and inflorescence final dry weights of the lateral shoot for 'Surf' chrysanthemums.

	Surf			
Treatment	Leaf dry weight (g)	Stem dry weight (g)	Inflorescence dry weight (g)	Total dry weight (g)
1-2[z]	1.06	0.65	1.44	3.35
1-4	1.04	0.64	1.41	3.40
1-6	1.17	0.71	1.35	3.23
1-8	1.22	0.69	1.22	3.18
3-2	0.76	0.46	1.28	2.50
3-4	0.78	0.41	1.02	2.21
3-6	0.79	0.44	0.96	2.19
5-2	0.62	0.37	1.04	2.03
5-4	0.70	0.31	0.97	1.88
7-2	0.74	0.33	0.99	2.06
Control	0.65	0.36	1.19	2.22
Waller-Duncan at 5% level	0.18	0.12	0.28	0.44

[z]First number refers to week at beginning of which high-temperature treatments were initiated and second number refers to length in weeks of high-temperature exposure.

High temperatures caused an increase in total leaf area and stem length as compared to low temperatures (Table 3-4). Increased leaf area was a result of an increase in leaf size and number. Increase in stem length was a function of increased node number as the mean internode length was not affected.

Effect of High Temperature on Floret Initiation and Differentiation

High temperatures delayed meristem transition to the reproductive state, floret initiation, and floret differentiation in 'Orange Bowl'. Involucral bract primordia, indicative of transition to the reproductive state, were evident at seven and 11 days after the start of short days for 'Orange Bowl' plants exposed to low and high temperatures, respectively. Statistical differences in meristem diameter between the temperature treatments were not evident for 'Orange Bowl' plants (data not shown). High temperatures decreased developmental rate from 1.7 rows of florets (control) initiated per day to 0.8 rows per day (Figure 3-1A). Exposure to high temperatures decreased the rate of perianth differentiation from 0.6 rows of florets per day (control) to 0.3 rows per day (Figure 3-1B). Transition to the reproductive state and rates of floret initiation and differentiation in 'Surf' were not significantly affected by high temperature treatments (data not shown).

Effect of High Temperature on Flowering

High temperature treatments beginning with week 1 or 3 of short days (treatments 1-4, 1-6, 1-8, 1-10, 3-2, 3-4, 3-6, and 3-8) increased the number of short days to showing-color and to open-flower for plants of 'Orange Bowl' and 'Surf' (Figure 3-2). The most sensitive 2-week period was the third and fourth weeks of short days. For treatments which provided only two weeks of high temperature exposure (treatments 1-2, 3-2, 5-2, and 7-2), treatment 3-2 caused the most delay. The amount of delay caused by treatment 1-4 was equaled by treatment 3-2 which overlapped the last two weeks of the 1-4 treatment.

Table 3-4. Effect of high (30°/26°C) and low (22°/18°) temperatures during short days on selected growth parameters of 'Orange Bowl' and 'Surf' chrysanthemums.

Cultivar	Treatment	Number of leaves (±SE)	Leaf area per leaf (cm^2) (±SE)	Internode length (cm) (±SE)	Total leaf area (cm^2) (±SE)	Stem length (cm) (±SE)
Orange Bowl	30°/26°[z]	20±1	12±0.5	1.1±0.2	245±4	22.6±1.0
	22°/18°	16±1	9±0.5	1.0±0.1	138±5	15.4±0.4
Surf	30°/26°	19±1	11±0.5	0.6±0.1	214±9	12.0±0.5
	22°/18°	16±1	9±0.5	0.7±0.1	147±6	11.4±0.6

[z]Day/night temperatures.

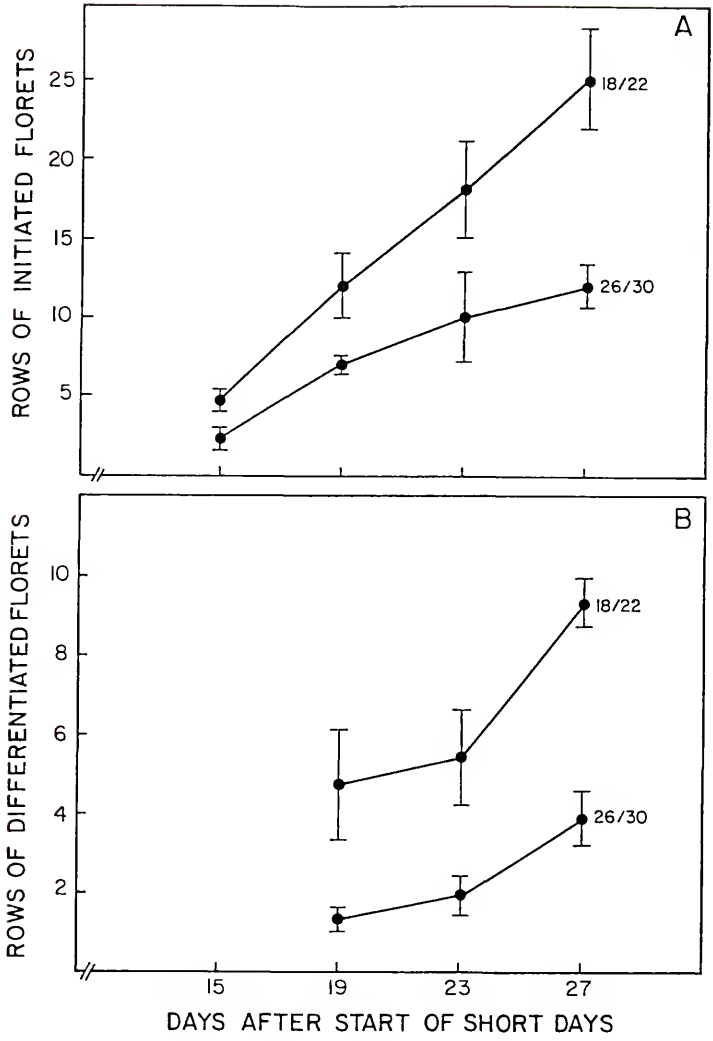

Figure 3-1. Effect of high (30°/26°C) and low (22°/18°) temperatures during short days on number of rows of florets initiated (A) and number of rows of florets with differentiated perianth (B) for 'Orange Bowl' chrysanthemums. Vertical bars represent S.E. of the means.

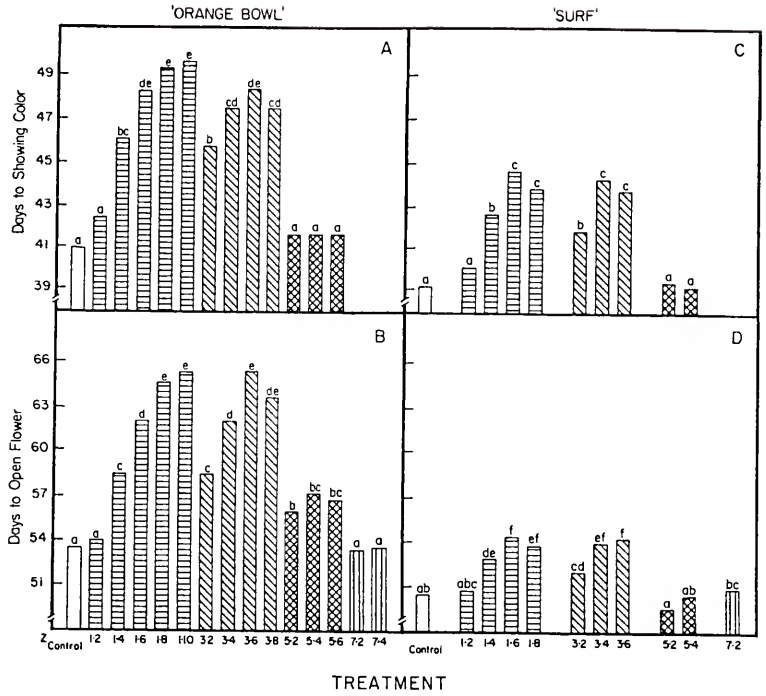

Figure 3-2. Effect of high- (30°/26°C) and low- (22°/18°) temperature treatments during short days on time to stage of showing-color and open-flower for 'Orange Bowl' and 'Surf' chrysanthemums. Bars with different letters are signficantly different at the 5% level according to Waller-Duncan Multiple Range Test. First number of treatment designation refers to week at the beginning of which high-temperature treatments were initiated and second number refers to length in weeks of high-temperature exposure.

Flowering was not delayed in plants of either cultivar exposed to high temperatures during the first two weeks of short days (treatment 1-2). Exposure to high temperatures starting with week 5 of short days (treatments 5-2, 5-4, 5-6) delayed flower opening in plants of 'Orange Bowl', but not of 'Surf'.

Cultivars differed in degree of developmental delay. 'Orange Bowl' plants exposed to longest high-temperature-duration treatment (treatment 1-10) flowered 12 days later than plants maintained at low temperatures (Figure 3-2B). 'Surf' plants exposed to high temperatures for the longest duration (treatment 1-8) flowered 3 days later than plants maintained at low temperatures (Figure 3-2D).

Treatments which included high temperatures during the third and fourth weeks of short days (treatments 1-4, 1-6, 1-8, 1-10, 3-2, 3-4, 3-6 and 3-8) resulted in bract formation interior to the outer rows of florets of 'Orange Bowl' plants. Noninvolucral bracts were evident and arrangement of outer rows of florets was disorganized by the fourth week of short days (Figure 3-3). 'Orange Bowl' plants exposed to high temperatures at the start of or at the third week of short days until flower (treatments 1-10 and 3-8) formed bracteate buds; i.e., only the outer rows of florets developed and the receptacle was covered with noninvolucral bracts. Secondary inflorescences arising from individual florets were also observed on plants forming bracteate buds (Figure 3-4). Increasing duration of exposure to high temperature increased the degree of teratological modifications. Concomitant with the increase in number of bracts was a decrease in the number of florets per inflorescence. Number of florets per inflorescence decreased with increasing duration of high temperature exposure (Figure 3-5). No teratological modifications were noted on 'Surf' plants.

Floret color of 'Orange Bowl' plants was affected by exposure to high temperatures after the seventh week of short days. Florets of plants exposed to

Figure 3-3. Meristem of 'Orange Bowl' chrysanthemum exposed to high (30°/26°C) temperatures for first 4 weeks of short days. Outer rows of florets are disorganized and noninvolucral bracts are evident.

Figure 3-4. Secondary inflorescence formed on a receptacle of 'Orange Bowl' chrysanthemum exposed to high temperatures (30°/26°C) from start of short days until week 10.

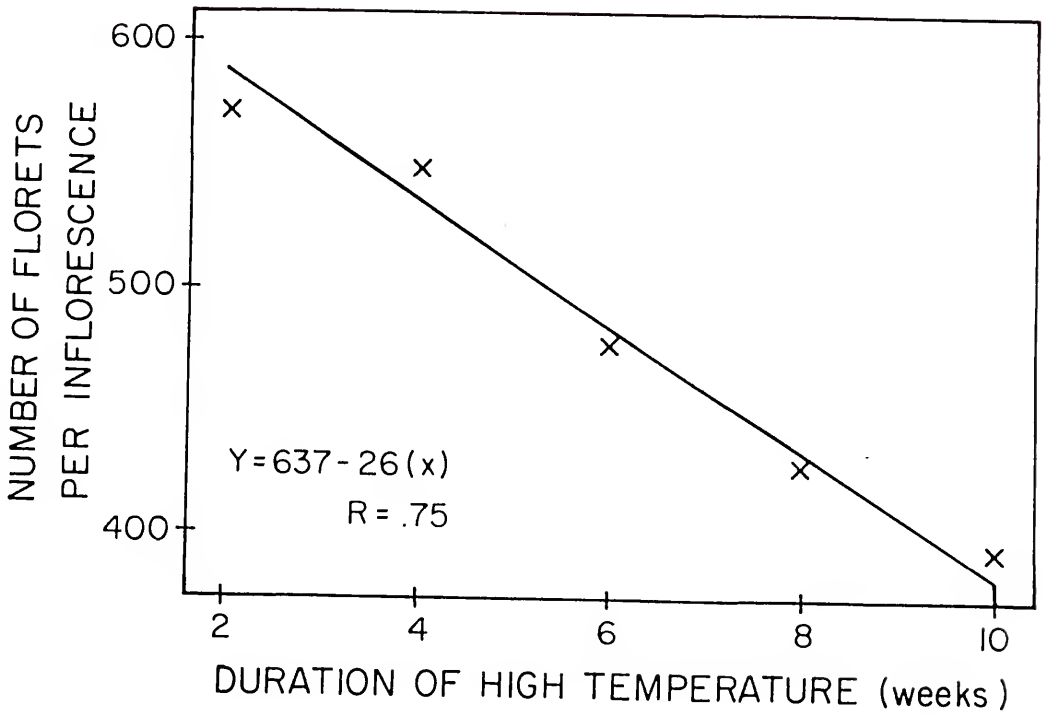

Figure 3-5. Effect of increasing duration of high (30°/26°C) temperatures during short days on mean number of florets per inflorescence for 'Orange Bowl' chrysanthemums. Plants were exposed to high temperatures at start of short days for 2, 4, 6, 8, or 10 weeks. Points represent treatment means with six inflorescences per treatment.

high temperature at this time (treatments 1-8, 1-10, 3-6, 3-8, 5-4, 5-6, 7-2 and 7-4) were yellow (Royal Horticultural Society color group 12A) rather than the normal orange-yellow (Royal Horticultural Society color group 14B) typical of the cultivar. The observed fading of floret color tended to increase with increasing duration of high-temperature exposure.

Our studies indicate that high temperatures during the short day photoinductive period enhanced vegetative growth and retarded floral development. The high temperature sensitive cultivar, 'Orange Bowl', was delayed in rate of floret initiation and differentiation by high production temperatures. Moreover, the supraoptimal temperatures used in this study perturbed floral development as evident in the induction of anomalous bracts on the receptacle and the decrease in the number of developed florets. The diminution in floret color may be attributable to either a decrease in synthesis or an increase in degradation of anthocyanins or carotenoids. The difference in tolerance or sensitivity to high temperatures is relative since 'Surf' was delayed by high temperature treatments, but not as severely as 'Orange Bowl', and abnormal development did not occur in 'Surf'.

Inhibition of floret initiation and/or development is a manifestation of indirect heat injury as defined by Levitt (112). Specific chemical and/or physical reactions may be inhibited or enhanced at supraoptimal temperatures. This form of injury is usually reversible; however, the duration of the exposure to supraoptimal temperatures is correlated with the length of time for development to resume (112). Exposure to high temperatures (38°) has been shown to alter the endogenous auxin and gibberellin levels in tomato (Lycopersicon esculentum Mill.) flowers and result in poor or inhibited fruit set (106). These high temperature effects may be due to altered or inhibited assimilate transport (60).

Kinet (102) has suggested that the inhibition of inflorescence development may be the result of competition for available assimilates between reproductive and vegetative growth. The redistribution of assimilates may be affected by various plant growth substances. It is thus hypothesized that the physical permutations of normal inflorescence development and the enhancement of vegetative growth in chrysanthemum may be attributed to pertubations in the normal balances of endogenous plant growth substances as a result of high temperatures.

CHAPTER IV
INVOLVEMENT OF SUPRAOPTIMAL TEMPERATURES AND PLANT GROWTH SUBSTANCES ON DEVELOPING INFLORESCENCES OF CHRYSANTHEMUM X MORIFOLIUM

Introduction

High-temperature exposure (30°/26°, day/night) promoted vegetative growth, delayed floret initiation and differentiation, and induced abnormal inflorescence development in Chrysanthemum X morifolium Ramat. 'Orange Bowl' plants (Chapter 3). The stages of inflorescence development most sensitive to high temperatures were floret initiation and early differentiation. Inflorescence development was unaffected by high temperatures after florets had differentiated perianth. The presence of interphasic structures indicated that the reproductive condition was unstable and the terminal regressed to the vegetative state. Apparently, the temperature optimum for vegetative growth is higher than the optimum for reproductive development in chrysanthemum (86).

Sub- or supraoptimal night temperatures reduced flower quality in carnation, Dianthus caryophyllus L. 'White Sim', by increasing petal number, resulting in a malformed flower referred to as a "bullhead" (73). The additional petals were located on secondary growth centers in the case of suboptimal night temperatures (5°), but arose directly on the receptacles of plants exposed to supraoptimal night temperatures (24.5°). Exogenous applications of GA and/or IAA to the developing apex during flower initiation promoted the development of secondary growth centers with additional petals, while kinetin applications increased the number of primary petals arising directly on the receptacle (73). Since petal number and secondary growth center development were observed to be

effected by either temperature or plant growth substances, Garrod and Harris (73) concluded that the effects of temperature might be mediated by alterations in the endogenous balances or levels of plant growth substances.

Low-temperature treatment (12°) prior to pistil and stamen differentiation increased the incidence of bullhead flowers in 'Baccara' rose (Rosa sp. L.) compared to higher, more optimal temperatures (18-24°)(126). Similar to carnations, bullhead is a malformation in rose in which the petals and petaloids are smaller, distorted, and more numerous than normal flowers (126). Zieslin et al. (196) found that bullhead flowers had lower gibberellin activity and higher cytokinin activity than normal flowers. Injecting gibberellic acid into the receptacles during low temperatures prevented malformations, and applications of cytokinins at optimal temperatures resulted in the characteristic symptoms expressed at suboptimal temperatures, i.e. a proliferation of adventitious florets (196). Thus flower development is contingent upon a cytokinin-gibberrellin balance during the stage of early flower development in rose (196).

Temperature influences the metabolic activity of plants (65). Supraoptimal temperatures may limit assimilate supply, hinder translocation or utilization of assimilates, and/or alter sink demand, thus inhibiting growth and development. These responses are probably regulated by endogenous plant growth substances as primary or secondary messengers of the environmental impingement. The objective of this study was to determine the effects of applied plant growth regulators on Chrysanthemum X morifolium 'Orange Bowl' exposed to supra- or optimal temperatures and to quantify changes in selected endogenous plant growth substances elicited by high temperatures.

Materials and Methods

Exogenously Applied Plant Growth Substances

Rooted cuttings of 'Orange Bowl' chrysanthemum were planted in a soilless growth medium (Metro Mix 300, W.R. Grace Co., Cambridge, MA) in 12.5-cm plastic pots. Plants were grown in a glass greenhouse providing a maximum photosynthethic photon flux (PPF) of 1200 μmol s^{-1} m^{-2} and maintained at 32±2° day and 21±2°C night temperatures. Noninductive photoperiods were provided for 2 weeks after planting. Plants were exposed to a 4-hour night interruption (2200-0200 hr) of approximately 10 μmol s^{-1} m^{-2} from incandescent filament lamps. Two weeks after planting, short-day photoinductive periods were initiated by providing a 15-hr nyctoperiod from 1700 to 0800 HR. An identical glass greenhouse was maintained at 38±2° day and 27±2° night temperatures.

Plants were fertilized weekly with 720 ppm N from a 20N-4.4P-16.6K commercial soluble fertilizer and irrigated as needed. Plants were pinched to seven leaves 1 week after planting and pruned to one lateral shoot when shoots were 3 to 4 cm in length. Leaves below the pinch were pruned to five per plant. At the start of the short-day photoinductive period, plants were randomly divided and grown in either the 32°/21° or 38°/27° greenhouse until flowering.

Chemical treatments were applied when three to four rows of florets were initiated as determined by dissection under a light microscope. This stage of development was chosen because of its sensitivity to high temperatures (Chapter 3). Chemical treatments were applied 7 days later to plants in high-temperature treatments than to plants in low-temperature treatments. A preliminary study indicated that chemical applications during floret differentiation were ineffectual (data not shown). Treatments were applied to the terminals of remaining plants as droplets of 0.5 ml per plant using 1-ml syringes. The treatments were $GA_{4,7}$

(GA_4-[1α,2β,4aα,4bβ,10β]-2,4A-dihydoxy-1-methyl-8-methylene gibbane-1, 10-dicarboxylic acid, 1,4A-lactone and GA_7-[1α,2β,4aα,4bβ,10β]-2,4A-dihydoxy-1-methyl-8-methylene gibb-3-ene-1, 10-dicarboxylic acid, 1,4A-lactone) at 500, 1000, or 2000 ppm; BA (6-N-benzylamino purine) at 75, 150, or 300 ppm; AVG (L-2-amino-4-[2-amino-ethoxy]-trans-3-butanoic acid), aminoethoxyvinylglycine, at 125, 250, or 500 ppm; ABA (abscisic acid) at 250, 500, or 1000 ppm; daminozide (butanedioic acid mono [2,2-dimethylhydrazide]) at 2500, 5000, or 10,000 ppm; and ethephon (2-chloroethylphosphonic acid) at 1000, 2000, or 4000 ppm. Tween 20 at a concentration of 0.05% was added to the chemical treatments and applied alone as a control. Plants in each greenhouse were in randomized complete block designs with six blocks per chemical treatment with one plant per block per treatment; the study was repeated three times over two years with similar treatments and environmental conditions. As the results obtained from these three studies were similar, only the results from the final study are reported.

Number of short days to first flower color (showing-color) and to when the outer rows of florets were perpendicular to the pedicel (open-flower) were recorded. At stage of open-flower, number of leaves, length of the lateral shoot, inflorescence diameter, number of florets, and number of noninvolucral bracts were recorded.

Enzyme-Linked Immunosorbent Assay for Zeatin Riboside

Four replicates of 24 rooted cuttings each of 'Orange Bowl' chrysanthemum were planted approximately 2 weeks apart and grown in glass greenhouses maintained at 32°/21° or 38°/27° as described previously. All cultural and environmental conditions were as previously described. Since the most high-temperature-sensitive stages were floret initiation and early differentiation (Chapter 3), terminal meristems from 10 randomly chosen plants

from each treatment per replicate were harvested when three to four rows of florets were initiated and when three to six rows of florets had differentiated perianth. Inflorescences from plants maintained under low temperatures were harvested at stage of floret initiation 5 to 7 days prior to high-temperature-treated plants and 5 to 6 days prior to high-temperature-treated plants at stage of floret differentiation. After determination of fresh weight, terminal meristems were ground in 80% ethanol, and extract was filtered, evaporated to dryness (35°), and re-extracted with water-saturated sec-butanol. Butanol layers were evaporated to dryness and brought to volume with water. The sample was adjusted to pH 3 to 4 with 2% NH_4OH and stored at 4°.

Linbro/Titertek EIA microtitration plates (Flow Laboratories, Inc., McLean, VA) were coated with monoclonal antibodies to zeatin riboside (Idetek, Inc., San Bruno, CA), and samples were assayed using a modified procedure by Eberle et al. (66). Wells of microtitration plates were filled with 200 μl of 250 μg/ml rabbit anti-mouse immunoglobulin (Sigma Chemical Co., St. Louis, MO) in 50 mM $NaHCO_3$ buffer, pH 9.5, and incubated at 4° for 24 hr. Wells were washed three times with a saline-Tween (0.5%) solution, pH 7.0, and then filled with 200 μl of monoclonal antibodies to zeatin riboside (100 μg/ml $NaHCO_3$ buffer) and incubated 24 hr at 4°. Wells were washed as before, then filled with 200 μl 10 mg/ml rabbit serum albumin in 25 mM Tris-buffered saline, pH 7.5, incubated for 1 hr at 25° and then rewashed. Duplicate standards and samples of each extraction were assayed. Immediately after the final wash, 100 μl of sample or 100 μl of trans-zeatin riboside (Sigma Chemical Co., St. Louis, MO) standard in Tris-buffered saline with 0.1% gelatin (w/v) were added to the wells with 100 μl of trans-zeatin riboside-alkaline phosphatase tracer (Idetek, Inc., San Bruno, CA) in Tris-buffered saline and incubated for 3 hr at 4°. To determine maximum and

nonspecific binding of the tracer, zero and excess (100 pmole/0.1 ml) of the trans-zeatin riboside standards, respectively, were also assayed in duplicate. Plates were washed as before with 0.5% saline-Tween solution. To determine phosphatase activity, 200 μl of a p-nitrophenyl phosphate, PNPP, solution (1 mg/ml 0.9 M diethanolamine buffer, pH 9.8) were added to each well and incubated for 1 hr at 37°. To each well, 50 μl of 1.0 M NaOH was added to stop the reaction. After 5 minutes, the optical density of each well was measured at 405 nm.

ACC Determination

Two replicates of 24 rooted cuttings each of 'Orange Bowl' chrysanthemum were planted 3 weeks apart and grown in glass greenhouses maintained at 32°/21° and 38°/27° as descibed previously. All cultural and environmental conditions were as previously described except plants were not pruned to one shoot per plant. Twenty-four terminal meristems from each temperature treatment per replicate were randomly harvested when three to four rows of florets were initiated, when three to six rows of florets had differentiated perianth, and when all florets had differentiated perianth. Inflorescences were harvested from low-temperature-treated plants 4 to 5 days prior to high-temperature-treated plants at stage of floret initiation, 4 to 6 days prior to high-temperature-treated plants at stage of floret differentiation, and 6 to 8 days prior to high-temperature-treated plants at stage of floret development. Mersitems were placed in vials in liquid nitrogen and stored at -86° until analysis.

After determination of their fresh weight, ACC was extracted from the terminal meristems and determined via a modification of the method of Lizada and Yang (115). Frozen meristems were homogenized and extracted overnight at 4° with two to three times their weight in cold 5%-aqueous sulfosalicyclic acid. The

homogenate was centrifuged at 27,000g for 25 minutes. The acidified supernatant was placed on a cation exchange resin (Rexyn 101 H^+) column (1 x 6 cm), washed, and eluted with four column volumes of 2N NH_4OH. Eluate was evaporated until dryness in vacuo at 38°, reconstituted to two times the original fresh weight in water, and assayed for ACC. To 500 μl of meristem extract in a 1.5-ml serum reaction vial was added 1 μmol of $HgCl_2$, and sufficient water to bring the final volume to 900 μl. Vials were sealed with serum caps, and 100 μl of a 4° mixture of 5.25% NaOCl and saturated NaOH (2:1, v/v) was injected. Vials were mixed on a Vortex and held in ice for 5 minutes and remixed. A 1-ml gas sample from the head space was injected into a gas chromatograph to determine ethylene content. Extracts from each treatment per replicate for each stage of floret development were assayed twice each with replicate internal standards. Amount of ACC present in the samples was based on the determined conversion efficiency of the internal standards.

Results

Exogenously Applied Plant Growth Substances

Number of leaves per lateral shoot was 20±1 on plants grown at 32°/21°, day/night and 24±1 on plants grown at 38°/27°. Chemical treatments could not affect the number of leaves within a temperature treatment, since time of application (floret initiation) was after leaf initiation had ceased. $GA_{4,7}$ applications to plants exposed to either temperature treatment greatly increased lateral stem length (Table 4-1). This increase was due to enhanced elongation of the uppermost internodes. Application of the higher rates of ethephon (2000 and 4000 ppm) reduced lateral stem length on plants exposed to high or low temperatures. Application of AVG, daminozide, or ABA at the highest rate (1000 ppm) reduced lateral stem length on plants exposed to low temperatures. Other

Table 4-1. Effect of low (32°/21°C) or high (38°/27°) temperatures during short days and exogenously applied chemical treatments at stage of floret intiation on lateral stem length and inflorescence diameter of 'Orange Bowl' chrysanthemums.

Treatment		Lateral stem length (cm) (±SE)		Inflorescence diameter (cm) (±SE)	
		32°/21°[z]	38°/27°	32°/21°	38°/27°
$GA_{4,7}$	500 ppm	41.3±1.2	60.2±1.6	11.8±0.6	9.2±1.2
	1000	44.2±1.4	59.6±0.9	12.0±0.4	8.6±1.3
	2000	43.9±2.1	65.8±2.5	11.5±0.6	10.0±0.0
Daminozide	2500	28.3±1.6	51.9±2.2	14.0±0.3	11.5±1.5
	5000	28.0±1.2	48.8±1.5	13.7±0.5	10.3±0.9
	10,000	25.2±1.0	47.3±2.0	13.8±0.4	11.5±0.6
BA	75	28.7±2.0	47.9±0.6	14.0±0.7	10.0±0.0
	150	28.4±0.9	50.9±1.4	13.6±0.3	11.0±0.1
	300	30.8±1.3	51.3±2.4	13.0±0.4	9.5±2.5
ABA	250	28.8±1.7	52.8±3.5	13.2±0.2	10.8±0.4
	500	27.3±2.1	49.3±1.6	12.9±0.4	10.3±0.8
	1000	26.7±0.5	49.8±1.7	12.8±0.5	11.0±0.5
Ethephon	1000	27.3±0.9	48.9±2.1	13.9±0.3	10.8±0.4
	2000	25.4±0.7	45.6±1.6	13.6±0.4	9.2±0.3
	4000	23.1±0.8	44.0±1.1	13.4±0.5	10.8±0.3
AVG	125	26.2±1.0	52.0±1.6	11.7±0.5	9.8±1.3
	250	22.0±0.9	49.7±2.4	12.7±0.5	10.8±0.3
	500	21.1±1.1	51.3±1.9	11.3±1.5	7.0±1.8
Control		28.6±0.9	51.3±2.8	13.5±0.2	10.0±0.9

[z]Day/night temperatures.

chemical treatments and rates did not affect lateral stem length. Nontreated plants in high-temperature treatments were almost twice as tall as similar plants in low-temperature treatments.

$GA_{4,7}$ or AVG applied to plants exposed to low temperatures and the highest rate of AVG (500 ppm) applied to high temperature-treated plants decreased inflorescence diameter compared to nontreated plants (Table 4-1). No chemical treatments increased inflorescence size. Inflorescence diameter of nontreated plants in high-temperature treatment was 10.0 cm; and inflorescence diameter of nontreated plants in low-temperature treatment was 13.5 cm.

Rate of inflorescence development was delayed by $GA_{4,7}$, ethephon, and AVG applications (Table 4-2). $GA_{4,7}$ and ethephon treatments on plants exposed to low-temperature treatments increased number of short days to stage of showing-color 1 to 2 days, but did not effect number of short days to open-flower. Plants exposed to high temperatures and treated with $GA_{4,7}$ were delayed 3 to 6 days to stage of showing-color and 5 to 7 days to open-flower compared to untreated plants. AVG treatments increased time to stage of showing-color and open-flower on plants exposed to either temperature treatment. Other chemical treatments did not affect rate of inflorescence development. Nontreated plants in low-temperature treatments flowered before similar plants in high-temperature treatments attained stage of showing-color.

The highest and lowest rates (500 and 2000 ppm) of $GA_{4,7}$ increased the number of florets on plants exposed to low temperatures, however, number of florets on plants exposed to high temperatures were not affected by $GA_{4,7}$ applications (Table 4-3). Number of noninvolucral bracts were increased by $GA_{4,7}$ and BA applications on low- or high-temperature-treated plants. BA treatments applied at the lowest rate (75 ppm) decreased the number of florets per

Table 4-2. Effect of low (32°/21°C) or high (38°/27°) temperatures during short days and exogenously applied chemical treatments at stage of floret initiation on number of short days to stage of showing-color and open-flower of 'Orange Bowl' chrysanthemums.

Treatment		Number of short days to stage of showing-color (±SE)		Number of short days to stage of open-flower (±SE)	
		32°/21°[z]	38°/27°	32°/21°	38°/27°
$GA_{4,7}$	500 ppm	39±0	60±1	50±0	78±0
	1000	40±1	59±0	50±1	76±1
	2000	40±0	62±1	50±1	78±1
Daminozide	2500	37±1	57±1	49±1	72±1
	5000	38±1	58±1	49±1	73±3
	10,000	39±1	58±2	51±1	70±1
BA	75	38±1	56±1	49±1	71±2
	150	38±0	55±1	50±0	72±2
	300	39±1	55±2	50±1	70±2
ABA	250	38±0	57±1	50±1	71±2
	500	38±1	56±1	49±1	70±1
	1000	38±1	56±1	50±1	70±2
Ethephon	1000	40±0	57±1	51±1	74±3
	2000	40±1	58±1	51±1	75±2
	4000	39±1	56±1	50±1	72±4
AVG	125	41±0	59±1	52±1	74±0
	250	41±0	60±1	51±0	73±2
	500	44±1	62±1	53±1	75±0
Control		38±0	56±1	50±0	71±2

[z]Day/night temperatures.

Table 4-3. Effect of low (32°/21°C) or high (38°/27°) temperatures during short days and exogenously applied chemical treatments at stage of floret initiation on number of florets and noninvolucral bracts per inflorescence of 'Orange Bowl' chrysanthemums.

Treatment		Number of florets per inflorescence (±SE)		Number of noninvolucral bracts per inflorescence (±SE)	
		32°/21°[z]	38°/27°	32°/21°	38°/27°
$GA_{4,7}$	500 ppm	390±27	165±12	71±14	173±26
	1000	373±37	222±9	55±20	168±10
	2000	365±14	162±26	86±14	169±23
Daminozide	2500	394±12	276±47	6±1	87±29
	5000	409±12	287±8	7±3	87±11
	10,000	451±40	301±15	9±5	99±7
BA	75	274±26	162±5	98±23	172±8
	150	305±22	128±17	75±15	214±33
	300	308±37	167±23	132±27	182±19
ABA	250	391±42	228±22	12±5	111±19
	500	384±61	254±32	10±4	158±80
	1000	372±31	276±37	17±4	117±27
Ethephon	1000	348±9	283±22	1±0	60±9
	2000	336±32	254±21	5±3	89±20
	4000	342±10	285±43	1±0	91±16
AVG	125	434±42	155±27	20±8	168±23
	250	382±27	168±43	21±7	263±33
	500	245±52	131±20	40±12	274±45
Control		331±19	211±35	5±2	114±29

[z]Day/night temperatures.

inflorescence on plants maintained at low temperatures, and BA applied at 75 or 150 ppm decreased the number of florets per inflorescence on plants maintained at high temperatures. Daminozide treatments did not affect noninvolucral bract number, but increased floret number on high or low temperature-treated plants. ABA treatments did not have an effect on number of florets at either temperature, however the highest rate of ABA (1000 ppm) increased the number of noninvolucral bracts on plants exposed to low temperatures. Ethephon was the only chemical treatment to reduce the number of noninvolucral bracts. Ethephon applied at the lowest and highest rates (1000 and 4000 ppm) essentially eliminated bract development on low-temperature-treated plants. On plants exposed to high temperatures, ethephon at the lowest rate (1000 ppm) decreased the number of bracts 47% compared to untreated high temperature plants, and floret number was also increased. The highest rate of AVG (500 ppm) decreased floret number on low- and high-temperature-treated plants. However, lower rates of AVG (125 and 250 ppm) increased floret number on plants exposed to low temperatures. AVG treatments enhanced noninvolucral bract development on plants maintained at both temperatures. Plants treated with $GA_{4,7}$, BA, or AVG and maintained at high temperatures had an equivalent or greater number of noninvolucral bracts compared to number of florets per inflorescence. The terminal inflorescences of these plants were considered bracteate buds, i.e., only the outer rows of florets developed and the receptacles were covered with noninvolucral bracts. Nontreated plants maintained under high-temperature conditions had 211 florets and 114 noninvolucral bracts per inflorescence. Nontreated plants maintained under low-temperature conditions had 331 florets and five noninvolucral bracts per inflorescence.

Enzyme-Linked Immunosorbent Assay for Zeatin Riboside

Endogenous zeatin riboside content increased with advancing stage of inflorescence development and with exposure to high-temperature treatment (Table 4-4). Endogenous zeatin riboside content increased between stages of floret initiation and differentiation 2.8 times and 2.1 times in inflorescences from plants maintained under low and high temperatures, respectively. Endogenous zeatin riboside content increased in inflorescences exposed to high-temperature treatment at stages of floret initiation 2.3 times and at floret differentiation 1.7 times compared to inflorescences exposed to low-temperature treatment.

ACC Determination

The level of ACC in the inflorescences was similar for plants exposed to low or high temperatures at stage of floret initiation (Figure 4-1). During stage of floret differentiation, a dramatic rise (4 times) in ACC content was observed in low-temperature-treated inflorescences. ACC content of high-temperature-treated inflorescences at stage of floret differentiation was not different from ACC content at stage of floret initiation. ACC content in both low- and high-temperature-treated inflorescences during stage of floret development were similar and were approximately half of determined ACC levels in inflorescences at stage of floret initiation.

Discussion

A primary response to heat stress may be an alteration in membrane integrity causing phytohormone imbalances (92). Gibberellin and auxin activities have been shown to decrease in response to high (38°) temperatures in tomato Lycopersicon esculentum Mill.) compared to low temperatures (24°-28°/17°-22°, day/night) (106). However, our studies indicate that gibberellin levels, activity, or sensitivity may increase in response to supraoptimal temperatures. $GA_{4,7}$

Table 4-4. Effect of low (32°/21°C) or high (38°/27°) temperatures during short days on endogenous zeatin riboside content of 'Orange Bowl' chrysanthemum inflorescences harvested at development stages: 1) floret initiation (three to four rows of florets initiated) and 2) floret differentiation (three to six rows of florets with differentiated perianth).

	Zeatin riboside (pMol·g fr wt^{-1}) (±SE)	
Stage of inflorescence development	32°/21°[z]	38°/27°
Floret initiation	237±71	545±180
Floret differentiation	662±53	1140±274

[z]Day/night temperatures.

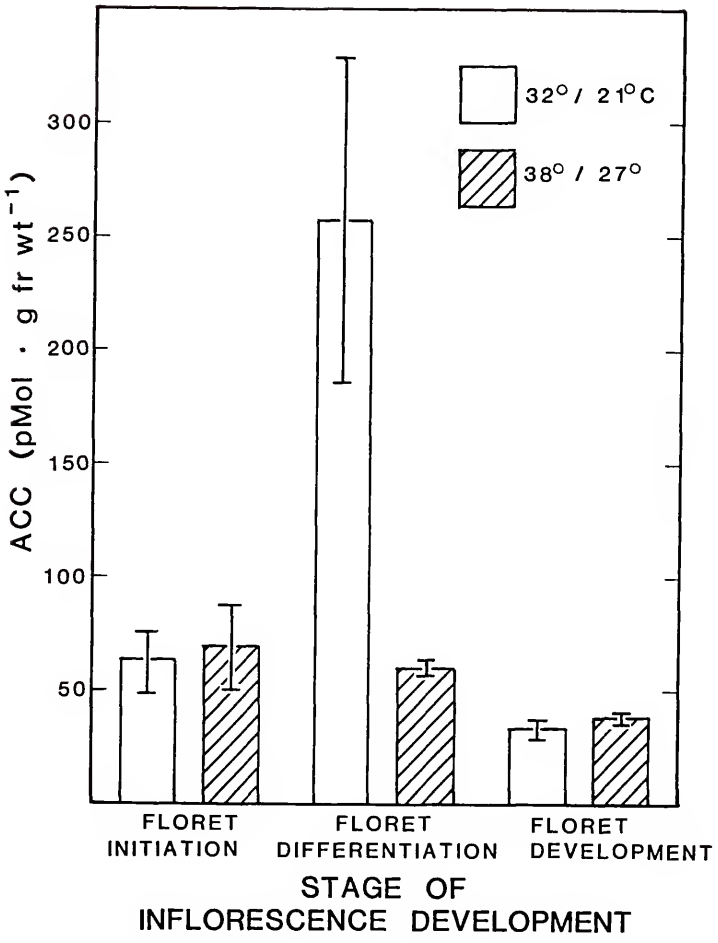

Figure 4-1. Effect of low (32°/21°C) or high (38°/27°) temperatures during short days on endogenous ACC content of 'Orange Bowl' chrysanthemum inflorescences harvested at developmental stages: 1) floret initiation (three to four rows of florets initiated), 2) floret differentiation (three to six rows of florets with differentiated perianth), and 3) floret development (all florets with differentiated perianth). Vertical bars represent SE of the means.

treatments were additive to high temperature treatments as applications to initiated chrysanthemum inflorescences increased lateral stem length, decreased inflorescence size, inhibited inflorescence development, and promoted bracteatebud development. Although daminozide applications did not appreciably affect chrysanthemum growth and development, floret arrangement of daminozide-treated inflorescences grown under high temperatures resembled untreated inflorescences in low-temperature treatments; exposure to supraoptimal temperatures distorts the spiral arrangement of florets (Chapter 3).

Cytokinins synthesized in the roots were suggested to be "protective substances" in heat-stressed plants (112). High temperature tolerance has been correlated with increased cytokinin activities in pea (Pisum sativum L.) (119). However, high temperature treatments decreased cytokinin activity in Phaseolus vulgaris L. cv. Great Northern and Begonia X cheimantha Everett cv. Prinsesse Astrid (92,195) and translocation in Zea mays L. cv. Inra 200 (9). BA treatments to chrysanthemum inflorescences promoted bracteate bud formation of low and high temperature-treated plants, and there was a marked increase in zeatin riboside content in response to high temperature treatment. It is thus proposed that gibberellin and/or cytokinin level, activity, or sensitivity increase in response to supraoptimal temperatures in chrysanthemums causing abnormal inflorescence development.

The optimum temperature for ethylene production in plant tissues is approximately 30° (186). Ethylene production is inhibited at temperatures above 35° in many fruits, and this inhibition is probably responsible for inhibition of fruit ripening at elevated temperatures (22). It appears that both ACC synthase activity (84) and the conversion of ACC to ethylene (186) are affected by supraoptimal temperatures. This inhibition of ethylene biosynthesis by high

temperatures may be caused by pertubations in cellular membranes, i.e. alterations in conformation of membrane-bound enzymes and/or membrane integrity, as stable, intact functional membranes are requisite for ethylene biosynthesis (8,113). In this system, ethylene appears to be necessary for normal inflorescence development, as AVG, a competitive inhibitor of ACC synthase, perturbed and ethephon treatments promoted normal inflorescence development. AVG applications reduced inflorescence size, retarded rate of inflorescence development, and promoted bracteate bud formation. Ethephon treatments inhibited vegetative growth and noninvolucral bract development on high-temperature-treated plants and floret arrangement of ethephon-treated inflorescences at high temperatures resembled untreated, low-temperature-treated inflorescences. The capacity for ACC production is correlated with the ethylene production capacity of the tissue (184,188). Thus the relatively high increase in ACC content on low-temperature-treated inflorescences during floret differentiation may indicate an integral and temporal role for ethylene in chrysanthemum inflorescence development.

CHAPTER V
SUMMARY AND CONCLUSIONS

High-temperature exposure (30°/26°, day/night) promoted vegetative growth, delayed inflorescence initiation and differentiation, and induced abnormal inflorescence development in Chrysanthemum X morifolium Ramat. 'Orange Bowl' plants. The stages of inflorescence development most sensitive to high temperatures were floret initiation and early differentiation. Inflorescence development was unaffected by high temperatures after florets had differentiated perianth. The presence of interphasic structures indicated that the reproductive condition was unstable and the terminal regressed to the vegetative state.

A primary response to heat stress may be an alteration in membrane integrity causing phytohormone imbalances (92). $GA_{4,7}$ treatments were additive to high-temperature treatments as applications to initiated chrysanthemum inflorescences increased lateral stem length, decreased inflorescence size, inhibited inflorescence development, and promoted bracteate bud development. Although daminozide applications did not appreciably affect chrysanthemum growth and development, floret arrangement of daminozide-treated inflorescences grown under high temperatures resembled untreated inflorescences in low-temperature treatments; exposure to supraoptimal temperatures distorts the spiral arrangement of florets. BA treatments to chrysanthemum inflorescences promoted bracteate bud formation of low and high temperature-treated plants, and there was a marked increase in zeatin riboside content in response to high temperature treatment. It is thus proposed that gibberellin and/or cytokinin level, activity, or sensitivity increase in response to supraoptimal temperatures in chrysanthemums

causing abnormal inflorescence development. In this system, ethylene appears to be necessary for normal inflorescence development, as AVG, a competitive inhibitor of ACC synthase, perturbed and ethephon treatments promoted normal inflorescence development. AVG applications reduced inflorescence size, retarded rate of inflorescence development, and promoted bracteate bud formation. Ethephon treatments inhibited vegetative growth and noninvolucral bract development on high temperature-treated plants and floret arrangement of ethephon-treated inflorescences at high temperatures resembled untreated, low-temperature-treated inflorescences. The capacity for ACC production is correlated with the ethylene production capacity of the tissue (184,188). Thus the relatively high increase in ACC content on low-temperature-treated inflorescences during floret differentiation may indicate an integral and temporal role for ethylene in chrysanthemum inflorescence development.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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